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Research Article

Variation in the Stabilimenta of *Cyclosa fililineata* Hingston, 1932, and *Cyclosa morretes* Levi, 1999 (Araneae: Araneidae), in Southeastern Brazil

Marcelo O. Gonzaga[1] and João Vasconcellos-Neto[2]

[1] *Instituto de Biologia, Universidade Federal de Uberlândia, Campus Umuarama, Bloco 2D, 38400-902 Uberlândia, MG, Brazil*
[2] *Departamento de Biologia Animal-IB, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970 Campians, SP, Brazil*

Correspondence should be addressed to Marcelo O. Gonzaga, mogonzaga@yahoo.com.br

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We investigated the characteristics of the stabilimenta constructed by two species of *Cyclosa*, describing the variations within and among five populations. Both species constructed stabilimenta composed entirely of silk (linear and spiral types) or of silk and debris (linear, detritus clusters and complex types). The vertical linear detritus type was the most frequent structure for adult females of both species, whereas stabilimenta consisting of detritus clusters were more frequent for juveniles of *C. morretes*. The latter structures appeared to be an intermediate state towards the linear continuous type usually found in adults. The other types were rarely found, and silk stabilimenta were to be constructed only when detritus was not available. The substitution of silk by detritus indicated that both materials function as camouflage in *C. morretes* and *C. fililineata* webs. The positions occupied by the spiders within the detritus column (and in some cases the orientation of the stabilimenta) varied markedly within populations, and the unpredictability of their location could be important in reducing the risks of predation. The hypothesis that stabilimenta constitute defensive devices was indirectly corroborated by the observation that spider's body width and length were, respectively, strongly correlated with the width and length of the stabilimenta.

1. Introduction

Stabilimenta are structures of silk or detritus included by some orbweaver spider species on the hub of their orbs or on the frame and anchor lines of the webs. These structures have appeared independently at least nine times during the evolution of orb-web spiders, always in species with webs that are exposed during the day [1, 2]. Herbestein et al. [2] found reports of web decorations in 22 genera of the families Araneidae, Tetragnathidae, and Uloboridae, but new records are continuously being added to this list (e.g., *Allocyclosa* [3, 4], *Molinaranea* [5], *Metepeira* [6], *Verrucosa*—M. O. Gonzaga, pers. obs.). Some stabilimenta, such as those of certain species of *Micrathena* and *Gasteracantha* (Araneidae), are generally composed of small silk flocks and are, therefore, considered by some authors to be nonfunctional structures [7]. Eberhard [8] argued that the placement of these silk flocks in the resting webs of *Gasteracantha cancriformis* and *Philoponella vicina* (Uloboridae) represent a strong evidence against prey attractant hypothesis for these structures but is compatible with the hypotheses of camouflage and web advertisement. Other stabilimenta, such as those of *Argiope* (Araneidae), are very conspicuous and have different shapes and sizes, depending on the age [9], size [10], and nutritional condition [11, 12] of the spiders.

Several species of *Argiope* show considerable within-species ontogenetic variation in the forms and frequency of decorations. Juveniles of *Argiope savignyi*, for example, usually construct discoid decorations, whereas adult females construct cruciate stabilimenta more often [7]. Schoener and Spiller [10] found that *A. argentata* of intermediate size build cruciate stabilimenta at a higher frequency than small and large individuals. These authors argued that the cruciate stabilimenta may serve to increase the apparent size of the spiders. Since lizards are major predators in their study areas (islands in Bahamas) and are gape-limited, spiders with a large apparent size may be less susceptible to attacks. Thus, large spiders would not need to appear still larger,

and small spiders would not build cruciate structures in order to avoid appearing like medium-sized spiders, which are a suitable prey for lizards. Li and Lee [13] showed that stabilimentum building and other web traits of *Argiope versicolor* change in response to the risk of predation. In that case, the presence of predator chemical cues induces the reduction stabilimentum area and frequency of construction by juveniles. The proportion of individuals that decorate their webs can also vary among populations. Hauber [14], for example, showed that only about 25% of *A. appensa* individuals from Guam built stabilimenta, whereas Kerr [15], who studied other populations of this same species on neighbouring Pacific islands, reported frequencies of web decorations that varied from 4% to 76%.

In the genus *Cyclosa*, most of the known species add web threads, debris (which is composed mainly of prey remains), and egg sacs to the central region of the webs to form linear continuous [16], linear discontinuous [17], spiral [18], or more complex structures (M. O. Gonzaga, pers. obs.). According to Nentwig and Heimer [7], each species has a specific stabilimentum pattern, but there have been few reports of intraspecific variation [2, 3, 16]. This variation may be very important when assessing the function of these structures. Craig [19, 20], for example, showed that the stingless bee *Trigona fulviventris* can learn to avoid the webs of *A. argentata* decorated with the same pattern of stabilimentum over successive days. When the orientation of these structures was varied, however, bees were more likely to be caught in the web threads. This finding indicates that an unpredictable decorating behaviour may reduce the probability that potential prey and/or predators and parasitoids will associate a specific pattern with the presence of a web.

The aims of this study were to determine whether there are species-specific patterns of stabilimenta in two *Cyclosa* species from southeastern Brazil and to describe the intraspecific variation of this structure within and among populations. We also tested whether stabilimentum measurements (width and length) follow the body size of their builders. The similarity between stabilimentum width and spider body width may be important to disrupt the contour and shape of spiders by blending individuals with the shape of the column of detritus, therefore reducing the probability of location by visually oriented predators. Likewise, increasing the length of the linear detritus structure during maturation, spiders may reduce the success of predators in locating their bodies within the stabilimentum. Finally, we investigated the process of reconstruction of stabilimenta after the removal of the original structure in order to assess whether some previously identified types of decorations were simply intermediate stages during the construction of other types.

2. Material and Methods

The samples were collected in five areas in southeastern Brazil, by visually searching along forest borders and within forests. The reserves ARIE Floresta da Cicuta (22°32′39″ S 44°05′22″ W), Parque Nacional Itatiaia (22°26′44″ S 44°36′43″ W), and Parque Estadual Intervales (24°16′38″ S 48°25′07″ W) are composed of old secondary growth and primary evergreen cloud forests (Mata Atlântica). In the Parque Estadual da Ilha do Cardoso (25°04′19″ S 47°55′30″ W), *Cyclosa fililineata* individuals were collected from cloud forests and the coastal sand dune vegetation (Restinga). The predominant vegetation types in Fazenda Rio Claro (22°46′22″ S 48°52′58″ W) are *Eucalyptus* plantations and secondary growth subtropical humid forests. Each area was sampled three times, with an interval of three months between consecutive surveys. This time interval was used to ensure that individuals in different stages of maturation were sampled.

The width (close to spider's position) and total length of the column of detritus, as well as the length of the upper and lower segments of the stabilimenta were measured for all of the webs that were located. Spiders and their stabilimenta were collected and latter measured in the laboratory using a dissecting microscope fitted with an ocular micrometer. To ensure that the dimensions of the stabilimenta remained unaltered during transportation, these structures were fixed to cardboard with a thin layer of glue.

The data obtained were used to compare the characteristics of stabilimenta between species and among populations and to calculate an index of symmetry of the detritus column using the equation: $IS = (((E/2) - A)/E) * 2$ (where E is total length of the column and A is distance between the spider and the upper extremity of the column). This index varied between -1 and 1. An index of 0 meant that the spider was located exactly in the middle of the column. In addition to the symmetry of the stabilimenta, we also recorded the inclination of these structures using a circular grid positioned behind the spider.

The Mann-Whitney U-test was used to compare the adjustment of abdominal width of the spiders with the width of the detritus column between *Cyclosa* species. The adjustment was calculated by subtracting the largest width of the abdomen from the width of the stabilimentum at the position immediately above the hub of the web. The relationship between abdominal width and the width of the stabilimentum and between spider body length and the length of the decorations were investigated by regression analysis using the pooled data of all populations for each species.

We also removed the stabilimenta of 56 individuals of *C. fililineata* and 48 individuals of *C. morretes* to study the process of rebuilding. For this, we completely destroyed the original webs and retained only the bridge thread, from which the spider started the construction of a new web. The web and stabilimenta parameters mentioned above were measured for the original web and at 24 h intervals after removal of the stabilimentum. These spiders were followed for a period of 120 h.

3. Results

Cyclosa fililineata and *C. morretes* built basically the same five types of stabilimenta: linear structures containing silk and

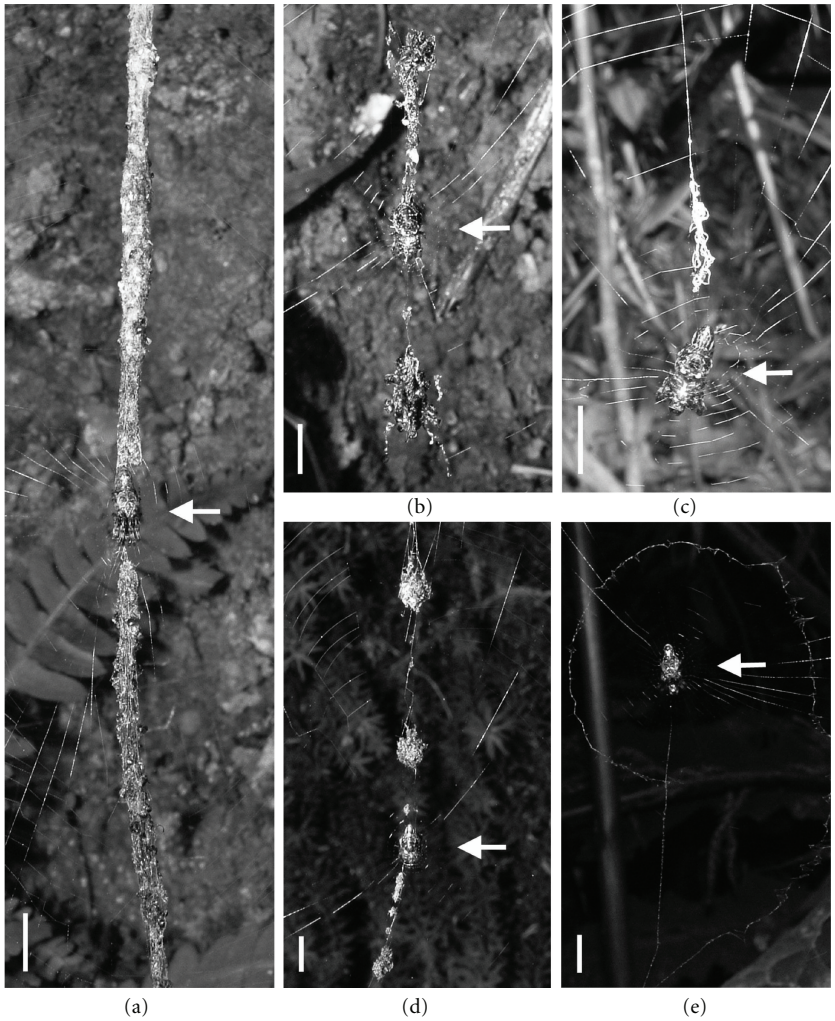

Figure 1: Decoration patterns in *C. morretes* and *C. fililineata* webs. (a) Linear detritus structure, (b) complex type with a linear segment and a blob resembling a large spider, (c) linear silk structure, (d) blobs of detritus forming a linear discontinuous structure, and (e) silk spiral. The arrows indicate the position occupied by the spider. Scales: 5 mm.

debris, incomplete columns characterized by one to many blobs of silk and debris, complex types (often resembling a large spider), spiral shapes composed only of silk, and linear silk structures (Figure 1). Adult females of both species constructed linear detritus columns more frequently than any other type of stabilimentum. However, linear discontinuous stabilimenta were very often found in webs of immature individuals of *C. morretes*. Complex detritus structures and both types of silk stabilimenta occurred only rarely in all of the populations studied (Figure 2).

The adjustment between the abdomen of the spiders and their stabilimenta was different for the two species (Mann-Whitney, $U = 6329.0, n_{C.\,fililineata} = 287, n_{C.\,morretes} = 80, P < 0.001$), with *C. fililineata* showing a better adjustment. The mean difference between the spiders and their stabilimenta in this species was 0.21 ± 0.15 mm, while in *C. morretes* the mean difference was 0.47 ± 0.37 mm. The dimensions of the stabilimenta varied with spider size. The width of the column close to the spider's position was strongly correlated with the abdominal width in both species ($r^2 = 0.49, F = 273.6, P < 0.001, n = 287$ for *C. fililineata* and $r^2 = 0.60, F = 118.1, P < 0.001, n = 80$ for *C. morretes*). Similarly, the length of the column was correlated with spider body length ($r^2 = 0.48, F = 368.5, P < 0.001$ for *C. fililineata*, and $r^2 = 0.42, F = 68.9, P < 0.001$ for *C. morretes*) (Figure 3).

The symmetry of the stabilimenta varied in all of the populations studied, especially in webs belonging to *C. fililineata*. Nevertheless, the extremities of the columns were always occupied less frequently than the central positions in this species (Figure 4(a)). *Cyclosa morretes* generally occupied the lower extremity of the column in Parque Nacional Itatiaia and in Parque Estadual Intervales. In Floresta da Cicuta,

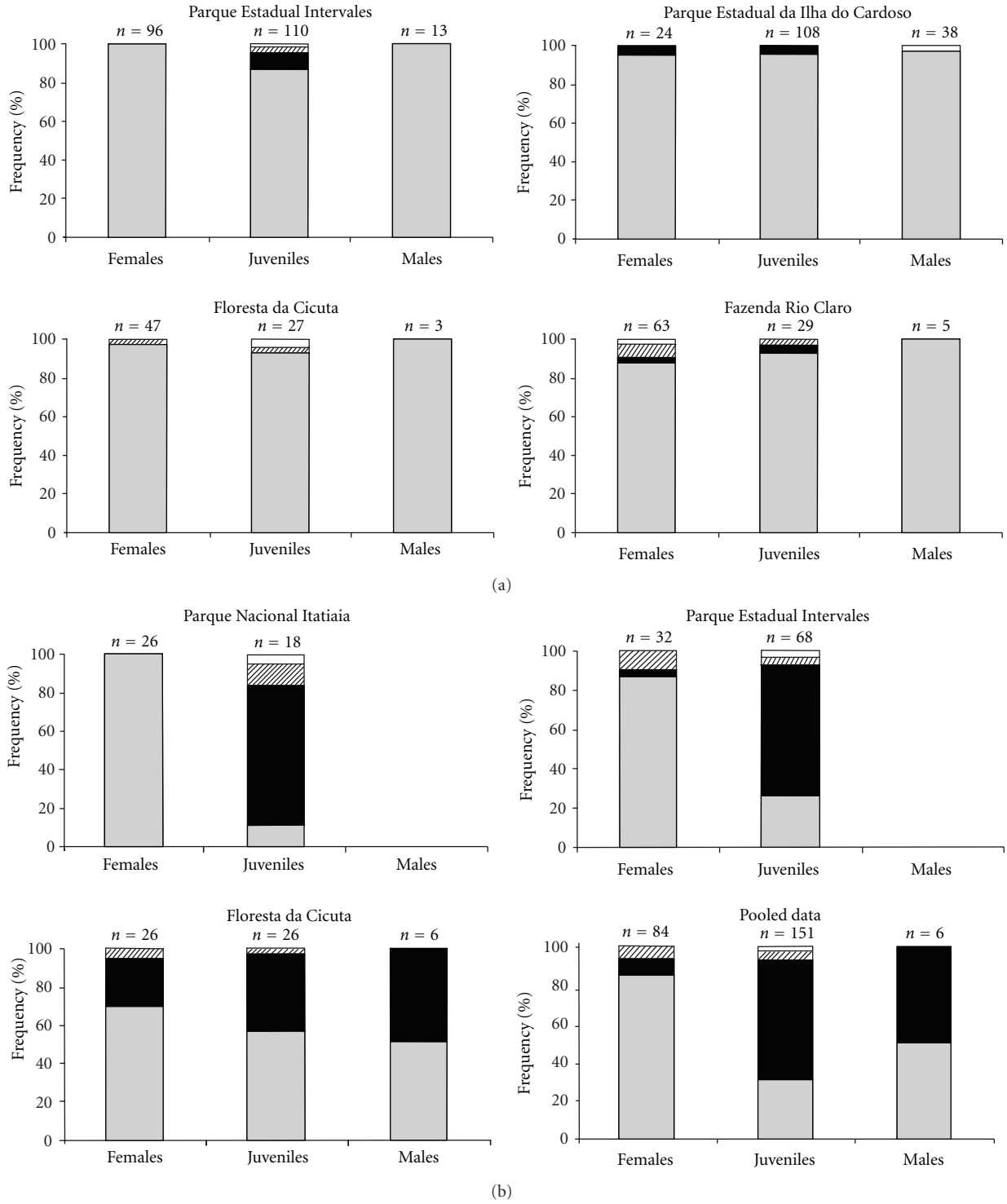

Figure 2: Frequencies of web decorations constructed by (a) *C. fililineata* and (b) *Cyclosa morretes* in the study areas. Grey bars: linear structures with detritus; black bars: linear discontinuous structures with detritus (blobs); bars with diagonal lines: complex types with detritus; white bars: linear silk + spiral silk stabilimenta.

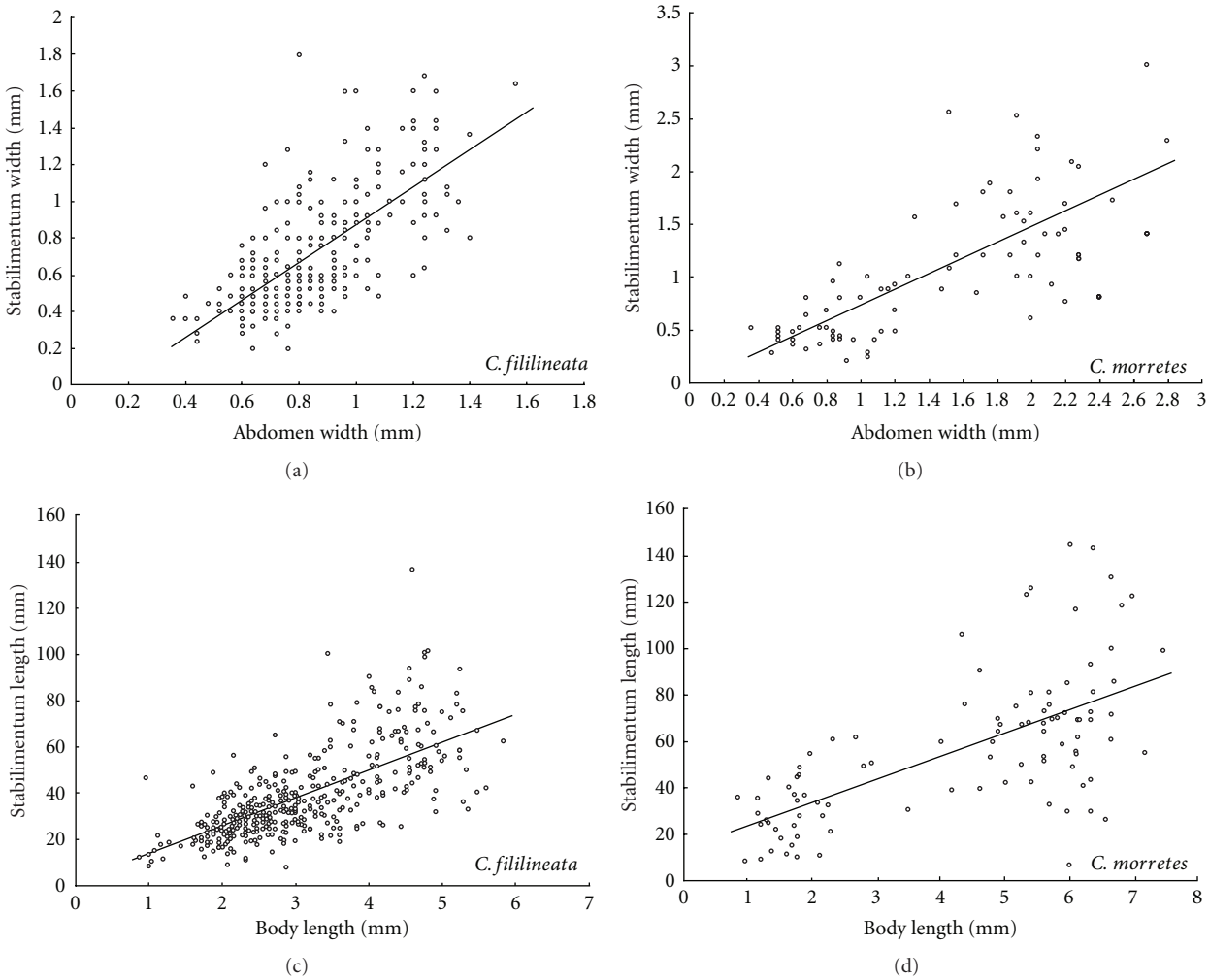

Figure 3: Relationship between abdominal width and the width of the linear detritus stabilimenta constructed by (a) *C. fililineata* and (b) *C. morretes;* and between body length and the length of the linear detritus stabilimenta constructed by (c) *C. fililineata* and (d) *C. morretes*. The points represent the pooled results for adults and juveniles from all populations.

however, we found several individuals in the lower extremity, but also a large proportion in central positions (Figure 4(b)). In all populations, most stabilimenta were constructed in a vertical position, but this orientation was not obligatory for these species (Figure 5).

The pattern of the original stabilimentum, in most cases a linear structure with detritus, was reconstructed within 72 h in most of the webs of *C. fililineata* (Figure 6). Several webs constructed the day after the removal of the original stabilimentum contained otherwise rare linear and spiral silk structures. The presence of silk stabilimenta on the first day after web destruction was also seen in *C. morretes*. However, in this species the frequency of linear detritus structures, even after 120 h, was still relatively low. Linear silk stabilimenta were gradually substituted by detritus as soon as the spiders had access to prey items or had collected debris intercepted by the web, but many individuals of *C. morretes* usually placed detritus far from the position occupied by the spider, creating discontinuous structures (Figure 7).

4. Discussion

All of the types of stabilimenta observed here in webs of *C. fililineata* and *C. morretes*, except for the complex shape with detritus, have been described for other species of this genus [3, 17, 18, 21]. Our comparisons among populations showed that the proportions of these types were similar for each species at different localities. Linear detritus structures were the commonest type constructed by *C. fililineata* and also by females of *C. morretes*. Unlike the discontinuous columns (blobs of detritus), this shape completely disrupted the visual sign of a spider. This could be an indication that the function of these stabilimenta is related to protection, possibly by reducing the probability of the spider being located by visually oriented predators. This disruptive function was supported by our results that showed a relationship between the stabilimentum width and the width of the spider's abdomen. The width of the column was generally similar to the size of the spiders, which helped to conceal their

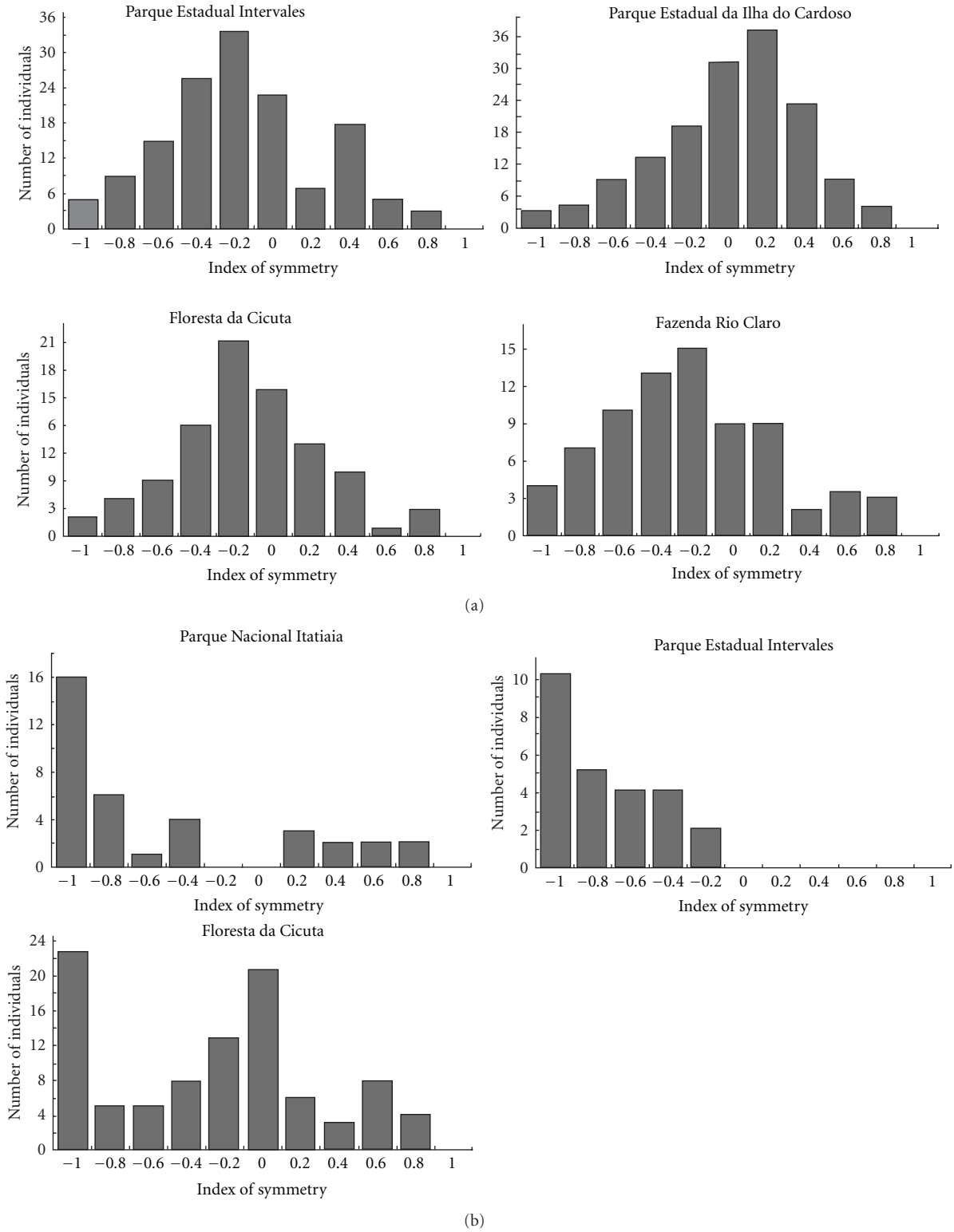

Figure 4: Positions occupied by adult (a) *C. fililineata* and (b) *C. morretes* in the detritus column in each population. −1: lower extremity, 0: center, +1: upper extremity.

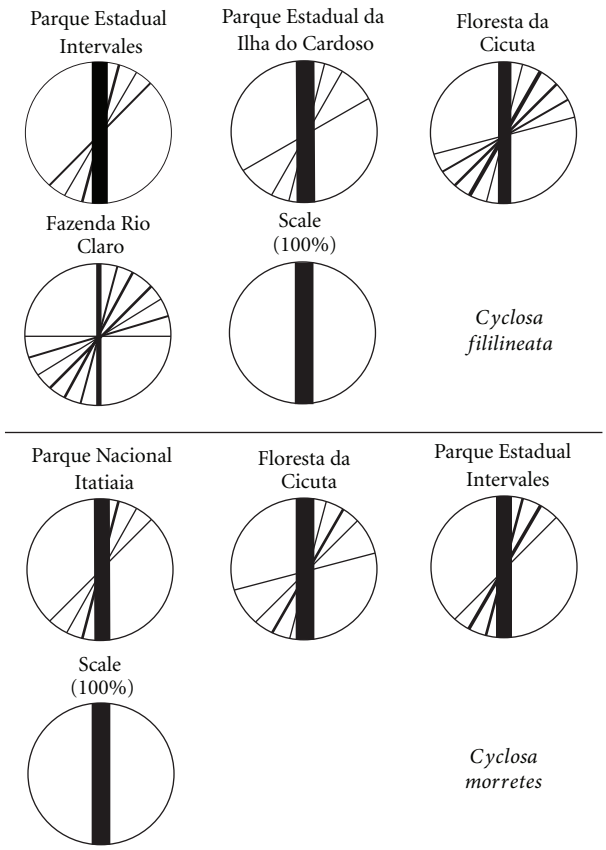

Figure 5: Frequencies of the inclinations of the stabilimenta constructed by *C. fililineata* and *C. morretes*. The inclinations were measured at 15° intervals and the thickness of each bar indicates the percentage of each category found in the field. Pooled results for juveniles and adults.

positions. Gonzaga and Vasconcellos-Neto [22] showed that artificial spider models (with about the same size of *C. morretes* females), attached to threads of nylon, were more attacked in the field than similar models in threads containing segments of modelling clay simulating stabilimenta. These results confirm that some predators were searching for prey items with the shape of a *Cyclosa* body and that columns with the same width of the spider body could reduce the risks of predation. Large spiders also build long columns, which is probably a consequence of the time they had to accumulate detritus and the availability of detritus after the consumption of relatively larger prey items. Long columns of detritus may be more efficient in reducing the probability of precise attacks by predators at the positions occupied by the spiders.

The placement of blobs of detritus, however, may also be a good strategy to avoid predators, especially when spiders have to deal with a very limited amount of detritus. The blobs were frequently about the same size as the spider and predators may be confused by this similarity during attacks. If the wrong target is attacked (a blob located far from the spider's body), the spider may have time enough to escape by running or jumping from the web. The complex type of stabilimentum appears to be a derivation of a blob but is larger and frequently contains projections resembling legs. We still do not have information on detritus acquisition rate and the suitability of particular types of debris to confirm the hypothesis that these types are associated to the availability of material to stabilimenta construction. Future work on these questions and comparing the survivorship of spiders with different stabilimentum types are important to determine the effectiveness of these structures against predators.

The variation in stabilimentum symmetry within several of the studied populations may be an indicative of a level of unpredictability that may be important in avoiding predators. There is no field evidence that spider predators use the stabilimenta to locate their prey [23]. Nevertheless, if this eventually occurs, the predators would have to locate the spider in the middle of the detritus column. By always attacking a specific position, predators will fail to capture prey most of the time. However, it is not clear why *C. morretes* occurs more frequently in the lower extremity of the detritus column. This position may allow a faster response after the detection of vibrational stimuli in the web, but we have no data to support or refute this hypothesis.

Another component of variability detected in this study was the orientation of the stabilimenta. Although most structures were constructed in a vertical position, there were stabilimenta that deviated from this direction in all of the studied populations. According to McClintock and Dodson [18], this variation in *C. insulana* may be related to the predominant orientation of elements in the background, thereby reducing the visibility of the decorations. In contrast, Rovner [17] showed that the orientation of the stabilimenta constructed by *C. turbinata* was determined exclusively by geotaxis. These divergent studies indicate that the causes and significance of variation in the direction of stabilimenta remain to be appropriately tested.

Herberstein et al. [2] argued that extrapolations from one phylogenetic group to another are unlikely to be relevant in resolving the debate about the functions of web decorations and that structures containing debris probably should not be considered as "decorations" or "stabilimenta," but as a separate behavioural phenomena. However, our results showed that the linear structures containing detritus constructed by at least two *Cyclosa* species were initially composed of only silk and were very similar to the linear stabilimenta of many uloborids. Eberhard [4] described the same pattern of substitution of one type of structure for another in *Allocyclosa bifurca* and in *Cyclosa monteverde*. In addition, he showed that these species do not construct silk stabilimenta when egg sacs are available. These findings suggest that the possible function of silk decorations can also be fulfilled by a structure containing egg sacs or detritus and that these different devices are variations of the same behavioural unit.

The observation that detritus is placed over silk stabilimenta (but never the opposite) argues against the hypothesis that the latter devices are used to attract prey. Detritus probably would interfere with any reflective property of the silk stabilimenta, thereby reducing their effectiveness in attracting insects searching for UV signals. Alternatively,

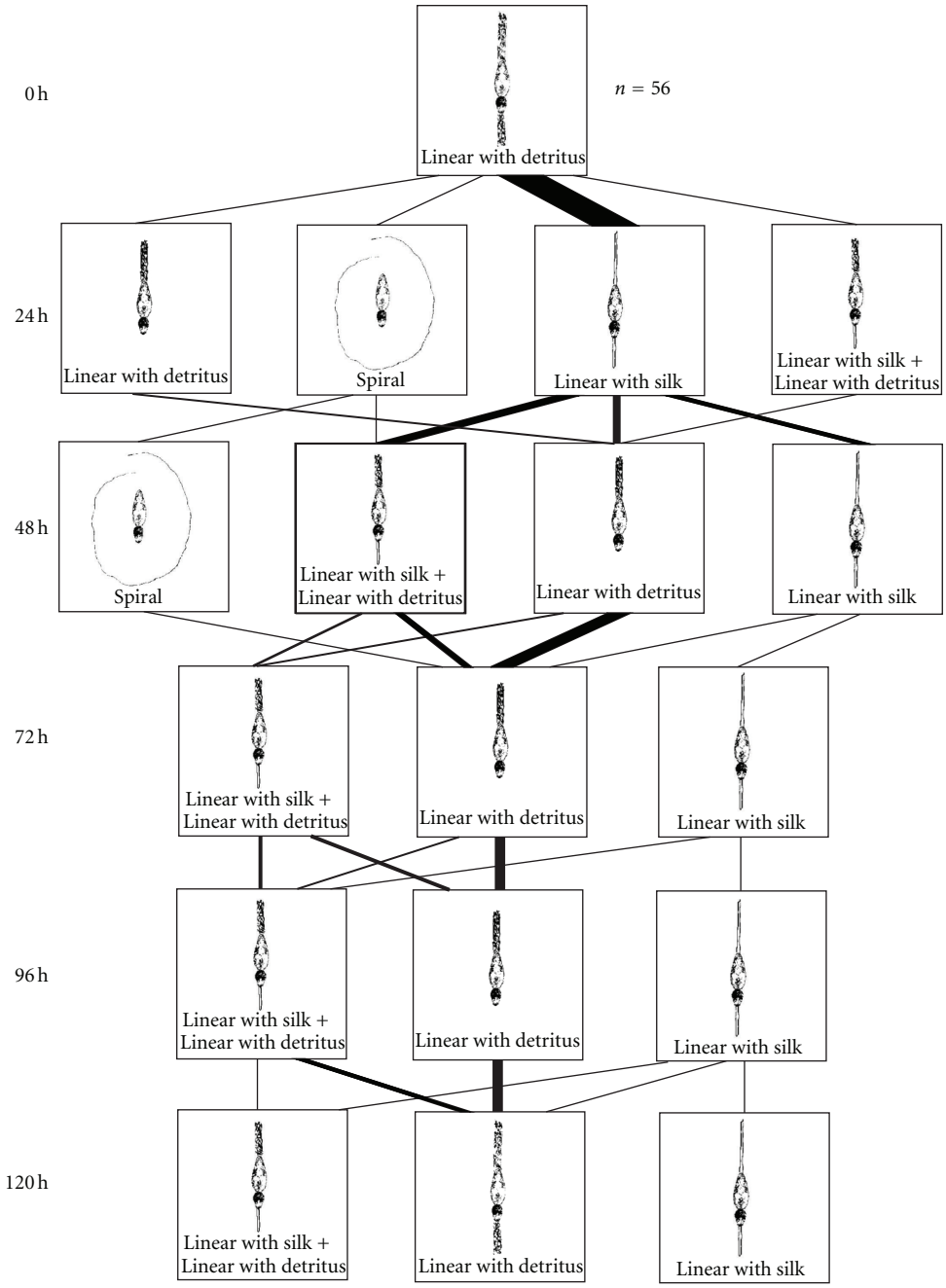

Figure 6: Reconstruction of stabilimenta by *C. fililineata*. The thickness of the lines indicates the number of webs that passed to the next stage.

linear and spiral silk stabilimenta may also disrupt the spider's shape but are soon replaced because they are probably less effective. At least to human eyes, spiders are easier located within silk stabilimenta.

Neet [24] argued that the spiral stabilimenta constructed by *C. insulana* may confer mechanical stability to orb-webs under strong wind. However, this conclusion was based solely on the observation that spiral stabilimenta were constructed at a higher frequency after stormy nights with strong winds. This observation could simply be a consequence of the higher incidence of web destruction under these weather conditions. Upon losing their original linear stabilimenta, spiders cannot build immediately another similar device because they do not have the detritus to incorporate into the webs. The hypothesis of mechanical stability must be tested by submitting webs with spiral and linear silk stabilimenta to controlled wind intensities and by measuring their resistance.

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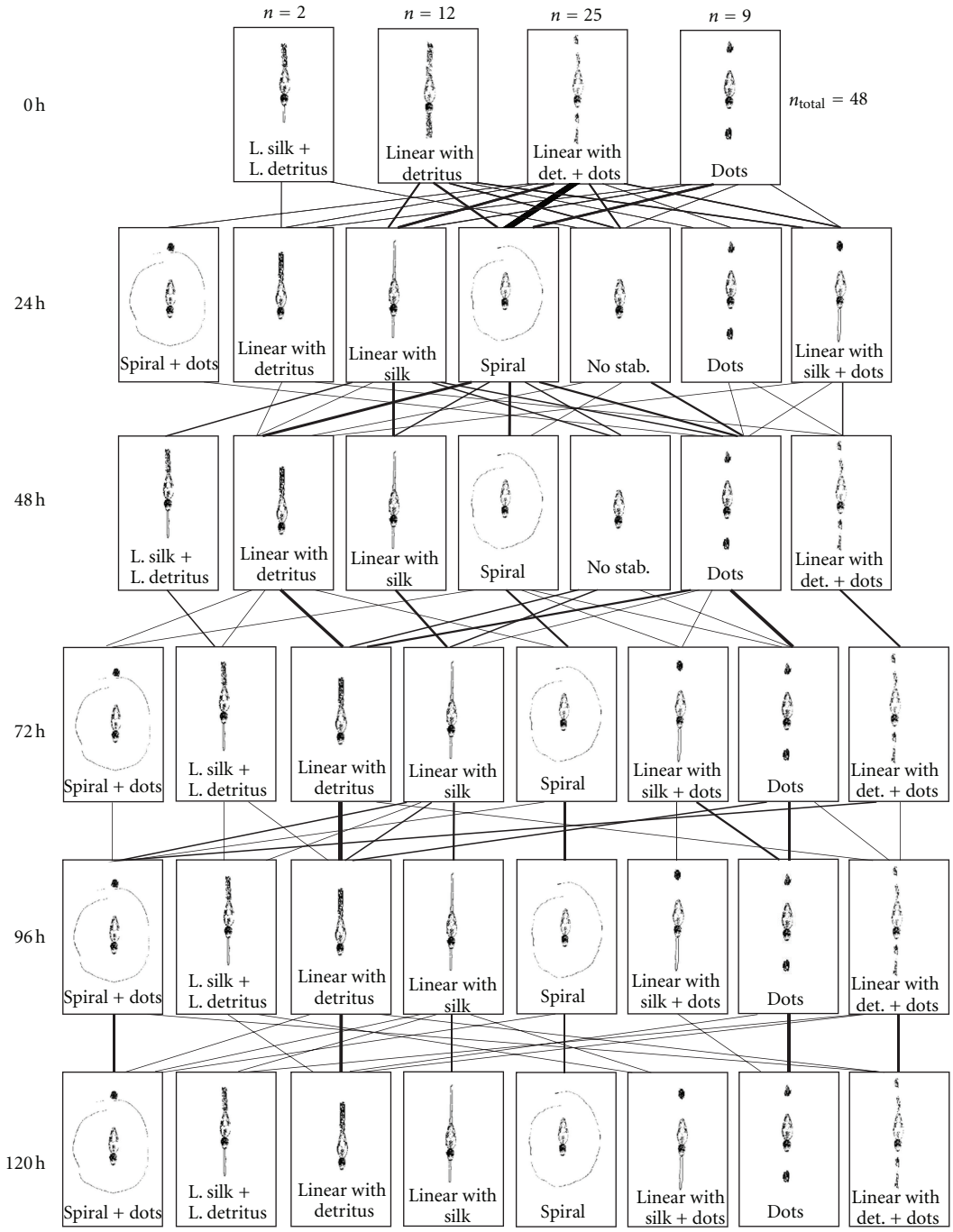

Figure 7: Reconstruction of stabilimenta by *C. morretes*. The thickness of the lines indicates the number of webs that passed to the next stage.

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